

MULTIVARIATE ANALYSES OF GEOGRAPHICAL VARIATION IN SOME AUSTRALIAN PASSERINE BIRDS: SIMULTANEOUS EXAMINATION OF SIX CHARACTERS

By IAN ABBOTT*

Department of Zoology, Monash University, Melbourne, Australia

Abstract

Canonical variates analysis was used to assess the patterns of interrelationships among populations of 19 species or superspecies of passerine birds in Australia. Six variates (bill length, bill depth, bill width, tarsus length, hallux length and wing length) were measured on nearly 4,000 specimens available in Australian museums. This multivariate approach permitted checking of the validity of presently accepted subspecies, and showed many to be gratuitous.

Isolated populations generally show a marked divergence from unisolated populations, and variation along eastern Australia in most species is very slight. In the majority of cases, patterns of variation within continental Australia are too complex to be worth naming sub-specifically.

In four out of six cases of species that are present on King Is., Flinders Is. and the Tasmanian mainland, the Tasmanian population is morphologically more similar to the population on King Is. than to that on Flinders Is. This is anomalous, because populations on Flinders Is. have had longer contact with populations on Tasmania, and this should have permitted gene flow between Flinders Is. and the Tasmanian mainland to be much more extensive.

Slight differences in morphology (and plumage) of populations do not necessarily mean such populations are best treated as subspecies; it is suggested that many populations, isolated in SW. Australia, the Tasmanian mainland and the Bass Strait islands (and treated as subspecies by modern taxonomists) may, in truth, be species. The difficulties of testing such an hypothesis are evident.

The main difference between the more traditional intuitive analysis of population variation and a multivariate study such as mine is the inconsistency of the former, because a difference between populations may be regarded as either of subspecific or of specific importance. With canonical analysis more characters are considered and differences are rigorously compared.

*Present address: Biology Department, McGill University, Montreal, P. Q., Canada.

Introduction

In this paper, a multivariate approach, through canonical analysis, to the taxonomy of some species of passerine birds in Australia is used. It differs from the traditional approach to taxonomy by objectively combining all characters at once to give maximum dispersion between samples. The standard (univariate) approach has been to examine variation within each character separately. At worst, differences and similarities have been evaluated subjectively; at best, a criterion of 75% or 90% separation (Mayr et al. 1953) has been used. Many of the subspecies described for Australian birds seem to have a tenuous basis. For example, *Sericornis humilis tregellasi* Mathews of King Is. was described because it differs from the Tasmanian mainland subspecies in

being lighter above (Mathews 1914). This subspecies and many others (not necessarily described by Mathews) clearly need evaluation with more sophisticated techniques.

In addition, the multivariate method probably better indicates the main patterns of interrelationships among populations, whereas the univariate method permits more detailed study of the characters actively responsible for the differences (Delany and Hcaly 1964). The univariate analysis of variation in the species studied here will be published elsewhere. The six variables measured in this study were bill length, bill depth, bill width, tarso-metatarsus length, hallux length and wing length. These were measured on all available specimens in Australia (see Acknowledgements) of 19 species or superspecies of passerines.

Multivariate treatments of biological variation are becoming more popular (Gould and Johnson 1972). Among the many applications to date, such analyses have been used to determine the probable affinity of early hominid bones (Rightmire 1972), and to study the taxonomy and evolution of mammals on islands (Foster 1965, Hope 1969), wolves (Jolicoeur 1959) and Red-winged Blackbirds (Power 1970).

Statistical Method

Suppose for any species that there are MG groups (or samples) of individuals, with M_i individuals in the i th group ($i = 1, \dots, MG$), and that on each individual six variables x_1, x_2, \dots, x_6 are measured (there is no provision for missing data). The set of these six measurements on each individual could be represented by a point in 6-dimensional space. Each of these MG groups are samples of 6-variate Normal universes (Seal 1966). Such a universe may be visualized as a swarm of points in 6-dimensional space centred at a point characterized by a mean vector and dispersed about that point as an ellipsoid characterized by a variance-covariance matrix. Each of the ellipsoids overlaps to some degree.

Using canonical analysis these data may be transformed into as few canonical variates as possible without losing any essential information. The following account of the technique is based on Armitage (1971), Dclany and Healy (1964), Hope (1969), Jolicoeur (1959), Seal (1966) and van de Geer (1971). Canonical variates analysis uses a linear discriminant function

$$C = c_1x_1 + c_2x_2 + \dots + c_6x_6 \text{ (Fisher 1936),}$$

where the coefficients c_i are arbitrary. Thus it would be possible to place one point C corresponding to each individual somewhere along an axis. However, in order that the groups can be discriminated as well as possible, the c_i 's are chosen such that the ratio

$$\lambda = \frac{\text{sum-of-squares between groups}}{\text{sum-of-squares within groups}}$$

is maximized. This can be done by solving the matrix equation

$$(B - W)c = 0,$$

where B and W are respectively the variance-covariance matrices of the six measurements between and within groups, and c is the required vector of coefficients (eigenvector). λ is called the eigenvalue or latent root.

The best linear function is that with c_i 's corresponding to the largest λ (call it λ_1). This function is called the first canonical variate I; it gives the best discrimination possible using a single linear function (it is equivalent to the linear discriminant function of many statistical texts (Seal 1966)). The second canonical variate II is that function with c_i 's corresponding to the next largest λ (λ_2). II is uncorrelated with I between and within groups. Six canonical variates exist.

If most of the variation between groups is explained by I and II, the ratios of sums-of-squares corresponding to III to VI (i.e. λ_3 to λ_6) will be relatively small, and may be neglected. The data may then be plotted as a scatter diagram with I and II as the x- and y-axes (Figs. 1-25). Any tendency for the groups to form clusters is then immediately obvious.

My original measurements were, following Seal (1966), transformed to common logarithms, and processed on a CDC 3200 computer in the Monash University Computer Centre using a program (CANON) based on one given by Hope (1969). A print-out of the program used, somewhat modified by J. Hope (*in litt.*), J. R. Bainbridge (pers. comm.) and myself, is found in Appendix 4.3 of Abbott (1972). The program was checked using Reeve's (1941) data as analysed by Seal (1966).

Since the canonical variates were standardized in the analysis (that is, were made independent of the units of the original measurements), the 90% confidence limit of each mean vector can be calculated as a circle of radius $(1.64/\sqrt{N})$, where N is the sample size. These were drawn in by Abbott (1972), but I now think that with such disparate sample sizes, it is better to leave them out.

The following constitute the samples used in these analyses.

- 1 N. Queensland (N. of latitude 20° S.)

- 2 S. Queensland (between latitudes 25 and 30° S.)
- 3 Queensland
- 4 Lord Howe Is.
- 5 E. New South Wales (between latitudes 30 and 35° S.)
- 6 Inland New South Wales (W. of Great Dividing Range)
- 7 Nowra
- 8 Canberra district
- 9 Victoria (includes SE. New South Wales S. of latitude 35° S.)
- 10 Deal Is. (between Wilsons Promontory and Flinders Is., Bass Strait)
- 11 Flinders Is.
- 12 King Is.
- 13 Tasmanian mainland
- 14 SE. South Australia and SW. Victoria
- 15 Mallee areas of E. South Australia and NW. Victoria
- 16 Murray and Lachlan river valleys in SW. New South Wales
- 17 Fleurieu Peninsula (includes Adelaide Plains and Mount Lofty Ranges)
- 18 Kangaroo Is.
- 19 Eyre Peninsula
- 20 Eyre and Yorke Peninsulas
- 21 Central Australia
- 22 S. Australia
- 23 S. Australia E. of Gulf St Vincent and including W. Victoria
- 24 W. Australia
- 25 SW. Australia
- 26 Shark Bay Islands

Distribution maps of the species studied in this paper may be found in Abbott (1972, Appendix 3). These maps show the geographical position of all specimens measured in this study.

The numbers above will be used in Figs. 1-25 to designate the samples used. The numbers of specimens in each sample for each species are listed in the Appendix.

Results

In interpreting the patterns in Figs. 1-25, it should be noted that the situation where the mean vectors ('points') of two populations fall close together does not necessarily mean those populations are conspecific. The only real, but

rarely feasible, test of whether a population is of a different species from another is whether the two interbreed. Thus, clustering of points or their scattering is to be interpreted as convergence and divergence in size of most of the six characters. There are few problems with using these patterns to examine the validity of described subspecies.

Malurus cyaneus and *M. splendens*

The twelve populations used fall into two basic groups (1) Tasmanian mainland and Bass Strait islands, (2) the rest (Fig. 1). Isolated populations tend to diverge from the nearest mainland population. Thus the points for Kangaroo Is. and Fleurieu Peninsula (18 and 17), Eyre Peninsula and Fleurieu Peninsula (19 and 17), SW. Australia and Eyre Peninsula (25 and 19), and Tasmanian mainland and Bass Strait islands and Victoria (13, 10, 11, 12 and 9) do not fall close to one another. There is a bigger difference between the Victorian and New South Wales (9 and 5) populations than there is between the New South Wales and Queensland (5 and 3) populations. This would support the taxonomic conclusions of Mack (1934) if it were not for the fact that the Queensland population (3) falls also near the populations from SW. New South Wales and the Fleurieu Peninsula (16 and 17). Such a situation seems impossible to name subspecifically.

The SW. Australian (25) population of *M. splendens* is the ecological equivalent of the eastern *M. cyaneus*, and may only be a well-marked isolate of the latter. That the Kangaroo Is. (18) point falls between the Tasmanian (13) point and the Australian main-

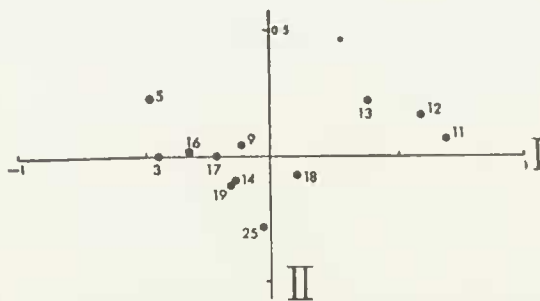


Fig. 1—Canonical analysis of variation in males of *Malurus cyaneus* and *M. splendens*.

land points is of interest, because Gould (1865) hinted that the Kangaroo Is. population might be referable to the Tasmanian form. The populations from the Bass Strait islands (11, 12) are longer-billed, longer-legged, etc., than that from Tasmania (13), but it seems scarcely worthwhile to bother naming them. The affinities of the Tasmanian population are with the King Is. (12), and not the Flinders Is. (11) population (Fig. 1).

Because the described subspecies of *Malurus cyaneus* are based on colour differences between adult males, I decided to check their validity by examining such differences with a large series of skins. Sixty-one species of adult males were sorted into groups based on the shade of blue on the back, and without looking at their geographical location. The skins were distributed geographically as follows: King Is. 4, Flinders Is. 3, Victoria 17, New South Wales 16, S. Queensland 11, Tasmanian mainland 7, Eyre Peninsula 1, Fleurieu Peninsula 2. Three groups were formed. A group containing dark blue specimens contained three of the King Is. specimens and one Flinders Is. specimen. A second group consisted of silvery-blue specimens: three from Sydney and eight from S. Queensland. The remaining group of 46 specimens showed a perfect gradation between the two extreme groups, but the gradation did not have a geographical basis. Clearly, subspecies erected on the basis of differences in colour are not satisfactory.

Sericornis frontalis superspecies and
Acanthornis magnus

The superspecies *S. frontalis* was formerly regarded (e.g. by Mathews 1930) as containing four species: *S. maculatus* from SW. Australia, Kangaroo Is. and S. Australia W. of the



Fig. 2—Canonical analysis of variation in males of *Sericornis frontalis* superspecies ● and in *Acanthornis magnus* ▲.

E. shores of Gulf St Vincent; *S. frontalis* from S. Queensland, New South Wales, Victoria, S. Australia W. to Fleurieu Peninsula, Deal Is. and possibly Flinders Is.; *S. laevigaster* from Queensland; and *S. humilis* from the Tasmanian mainland, King Is. and Flinders Is.

The 11 male populations plotted in Fig. 2 fall into three clusters. The Tasmanian mainland, King Is. and Flinders Is. (13, 12, 11) points fall to the right; these populations consist of large individuals. Because of small numbers and unsexed material it was necessary to lump sexes of the Deal Is. (10) population. Even so, the point falls nearer to the Flinders Is. (11) point than to the Victorian (9) point. The Tasmanian population (13) falls with the King Is. (12) population.

The point representing the populations on the Shark Bay islands (26) (Dirk Hartog and Bernier islands) falls well to the left of the SW. Australian (25) point. In the intermediate cluster of points, there is little to distinguish the SW. Australia, Fleurieu Peninsula, Kangaroo Is., Queensland, New South Wales and Victorian (25, 17, 18, 3, 5, 9) points. Generally, the points for geographically close populations fall near one another. The Queensland (3) point falls nearer the Kangaroo Is. (18) point.

Because most specimens are unsexed, it was necessary to lump the sexes of *Acanthornis magnus* from Tasmania. The point (▲ 13) for

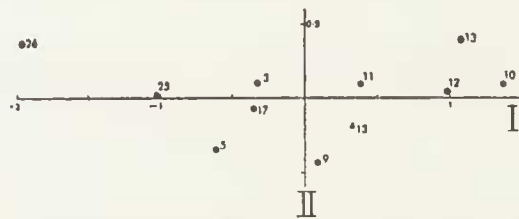


Fig. 3—Canonical analysis of variation in females of *Sericornis frontalis* superspecies ● and in *Acanthornis magnus* ▲.

this population falls with the intermediate *Sericornis* group. *Acanthornis magnus* is sometimes regarded as the senior member of a double invasion with *Sericornis* into Tasmania. It is perhaps better treated as a *Sericornis* (Keast 1968).

The female populations (Fig. 3) show a

similar trend to the males, thus giving support to the above interpretation. That males probably predominate in the lumped populations on Deal Is. (10), and for *Acanthornis* in Tasmania (▲ 13) is evident from the positions of these points in Fig. 3.

Thus, apart from that on Kangaroo Is. (18), all the populations of *Sericornis* sens. str. from islands differ markedly from the nearest mainland populations. It also seems unnecessary to distinguish subspecifically any of the populations in the intermediate cluster in Figs. 2-3.

Acanthiza pusilla superspecies and *A. ewingi*

The genus *Acanthiza*, and especially the superspecies *A. pusilla*, have long been the despair of Australian taxonomists, such as Mack (1936) and Mayr and Serventy (1938). The reason for this is very obvious from Figs. 4-5. The populations are poorly discriminated, and even if the points were plotted in 6-dimensions the discrimination would hardly be improved (Abbott 1972, Appendix Table A5.3). Because of poorly sexed material, it was necessary to lump sexes from Central Australia.

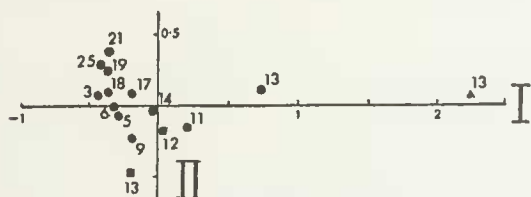


Fig. 4—Canonical analysis of variation in males of *Acanthiza pusilla* superspecies ●, *A. ewingi* ■, and in *Acanthornis magnus* ▲.

Geographically close populations fall near to one another in Fig. 4, and populations at both ends of the geographical range overlap least. Differences between *Acanthiza* populations are minimized in Fig. 4; *Acanthornis* was included since in some features it more closely resembles *Acanthiza* than *Sericornis* (Campbell 1900, D. Milledge pers. comm.). Morphologically, it is clear that *Acanthornis* is unlike *Acanthiza*. In Fig. 5 (females), dispersion between the *Acanthiza* samples is maximized.

In Fig. 5, the point (13) representing *A. pusilla* from Tasmania is well separated from

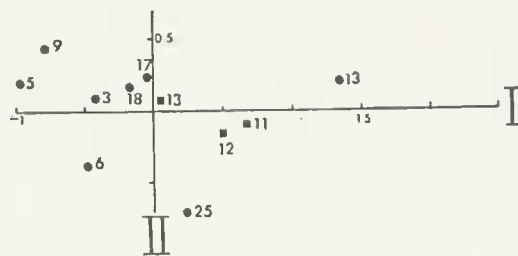


Fig. 5—Canonical analysis of variation in females of *Acanthiza pusilla* superspecies ● and *A. ewingi* ■.

the Victorian (9) point. The points for *A. ewingi* on the Bass Strait islands (■ 11, 12) fall between those for *A. ewingi* from Tasmania (■ 13) and *A. pusilla* from Tasmania (13). The point (25) for SW. Australia falls away from that (17) of Fleurieu Peninsula.

It is probably reasonable to infer that there is very little difference between populations throughout mainland Australia, except that the SW. Australian population appears distinct from that of the Fleurieu Peninsula. According to McGill (1970), the *A. pusilla* superspecies is divided into *A. apicalis* from SW. Australia and Eyre Peninsula across to inland New South Wales, and *A. pusilla* from Queensland, New South Wales, Victoria, Fleurieu Peninsula, SE. Australia, Kangaroo Is., King Is. and the Tasmanian mainland. *Acanthiza ewingi* is found only on King Is., Flinders Is. and the Tasmanian mainland.

Acanthiza ewingi from Tasmania is morphologically more similar to *A. ewingi* on King Is. than on Flinders Is. King Is. is also like Tasmania is that it has *Acanthornis magnus* and *Acanthiza pusilla*, neither of which is known from Flinders Is.

Acanthorhynchus tenuirostris superspecies

The E. Australian populations (N.S.W., Vict., Qd. 5, 9, 3) converge morphologically,

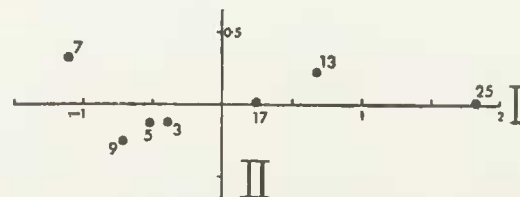


Fig. 6—Canonical analysis of variation in males of *Acanthorhynchus tenuirostris* superspecies.

showing increased size in the characters studied (Fig. 6). The SW. Australian population (*A. superciliosus*, 25) consists of small individuals, and falls nearest to the Tasmanian (13) population. The Fleurieu Peninsula (17) population is intermediate between Tasmania (13) and the E. coast group (3-9). The SW. Australian population (25) is thus quite distinct from the geographically nearest population from the Fleurieu Peninsula (17), as is Tasmania (13) from Victoria (9) and the Fleurieu Peninsula (17) from Victoria (9). This is the first case in which the isolated populations trend toward small size in most of the six characters studied (in *Sericornis* only one isolated population—that of the Shark Bay islands—tended to small size in the characters studied).

I cannot explain the separation between the New South Wales (5) and Nowra (7) points (Figs. 6-7). The trends for the female populations (Fig. 7) broadly agree with those described above for males.

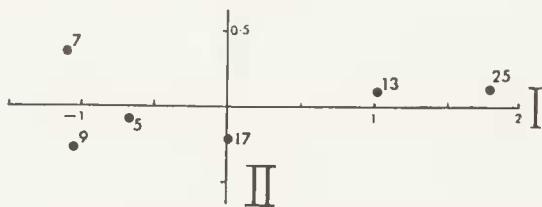


Fig. 7—Canonical analysis of variation in females of *Acanthorhynchus tenuirostris* superspecies.

The latest revision of this superspecies recognized seven subspecies (Salomonsen 1967). These are from N. Queensland, SE. Queensland, New South Wales-Victoria-SE. South Australia, Kangaroo Is., Fleurieu Peninsula, Bass Strait islands, and Tasmanian mainland. The Queensland subspecies seem unnecessary.

Melithreptus lunatus superspecies and *M. gularis* superspecies

The *Melithreptus lunatus* superspecies consists of *M. lunatus* from mainland Australia and Deal Is., and *M. affinis* from the Tasmanian mainland, King Is. and Flinders Is. The *M. gularis* superspecies is made up of *M. gularis* and *M. laetior* from mainland Aus-

tralia, and *M. validirostris* from King Is., Flinders Is. and the Tasmanian mainland.

The three E. coast populations of *M. lunatus* (Qd., N.S.W., and Vict. 3, 5, 9) fall very close to one another (Figs. 8-9). Only the isolated populations show any deviations from these. The SW. Australia (25) population converges with *M. gularis* from Queensland (■ 3, Fig. 8)

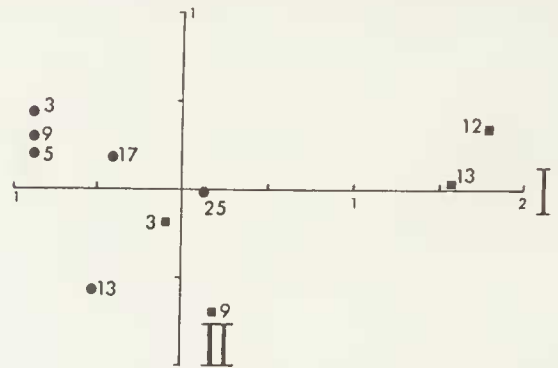


Fig. 8—Canonical analysis of variation in males of *Melithreptus lunatus* superspecies ● and *M. gularis* superspecies ■.

by being larger. The Tasmanian (13) point falls somewhat farther from the Victorian (9) point than does the SW. Australian (25) point from that of Fleurieu Peninsula (17, Fig. 9). The Fleurieu Peninsula (17) point falls nearer to the Victorian (9) point. These findings suggest that it would be more consistent to treat both the Tasmanian and SW. Australia populations (13 and 25) either as subspecies of *M. lunatus* or as different species from *M. lunatus* (see discussion).

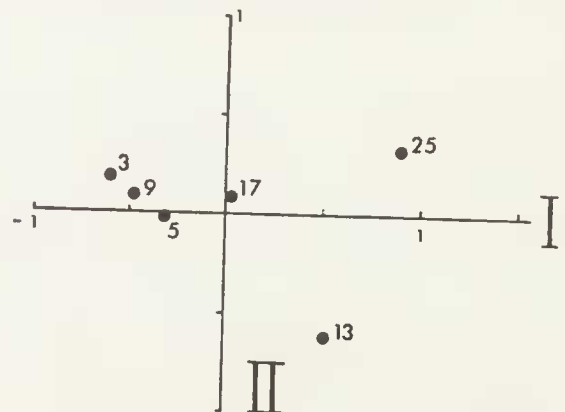


Fig. 9—Canonical analysis of variation in males of *Melithreptus lunatus* superspecies.

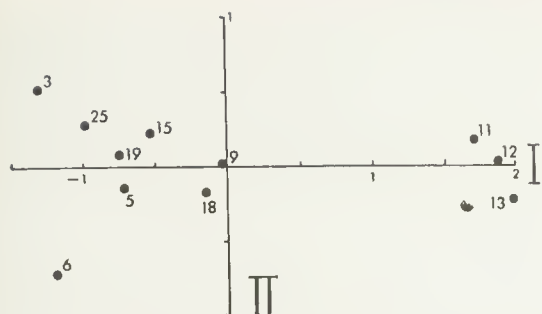


Fig. 10—Canonical analysis of variation in males of *Meliphaga leucotis* superspecies.

With the *M. gularis* superspecies, the isolated populations for which I have data (Tasmanian mainland and King Is. 13 and 12) are greatly different from the two mainland populations for which I have data (Qd. and Vict. 3 and 9) (Fig. 8).

Salomonsen (1967) recognized only two subspecies of *M. lunatus*, one from SW. Australia, and the other from the rest of the range. He also recognized two races of *M. affinis*, Tasmanian mainland and the Bass Strait islands. I do not have enough material to check the latter. He recognized no subspecies of *M. gularis*, but for *M. validirostris* recognized one for the Bass Strait islands and another for Tasmania. This may be unnecessary (Fig. 8).

Meliphaga leucotis superspecies

The points fall into two clusters (Figs. 10-11). The Tasmanian mainland and Bass Strait island populations (11, 12, 13) show a nett increased size in the characters studied. The Tasmanian (13) point falls nearer King Is. (12) than to Flinders Is. (11). Variation in the mainland populations follows no obvious

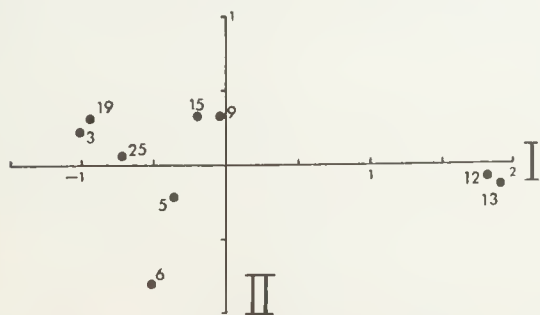


Fig. 11—Canonical analysis of variation in females of *Meliphaga leucotis* superspecies.

trend. The populations from SW. Australia, Eyre Peninsula and Queensland (25, 19, 3) converge, and the inland New South Wales (6) point falls by itself, and not with that (15) of the Mallee areas of NW. Victoria and E. South Australia (Figs. 10-11). It is impossible to satisfactorily name this kind of variation. However, Salomonsen (1967) recognized two subspecies of the mainland *M. leucotis* (from SW. Australia, and the rest of

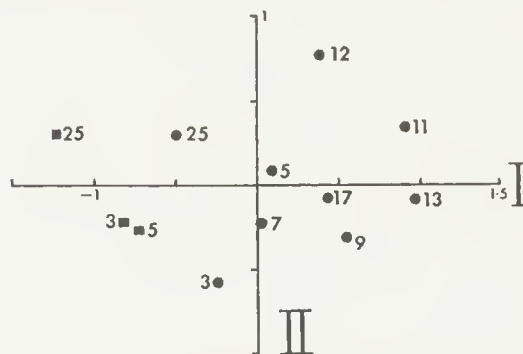


Fig. 12—Canonical analysis of variation in males of *Phylidonyris novaehollandiae* ● and *P. nigra* ■.

the range). This is not supported by this study. He recognized no subspecies of *M. flavicollis*. My study supports this.

Phylidonyris novaehollandiae and *P. nigra*

There is no tendency for the points (13, 12, 11) representing the Tasmanian, King Is. and

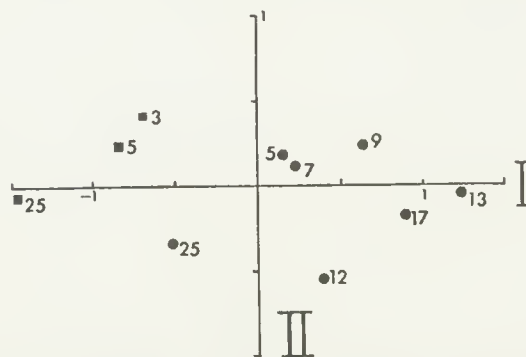


Fig. 13—Canonical analysis of variation in females of *Phylidonyris novaehollandiae* ● and *P. nigra* ■.

that of the Flinders Is. (11) population. Little Flinders Is. populations to cluster (Figs. 12-13). The Tasmanian (13) point falls nearer

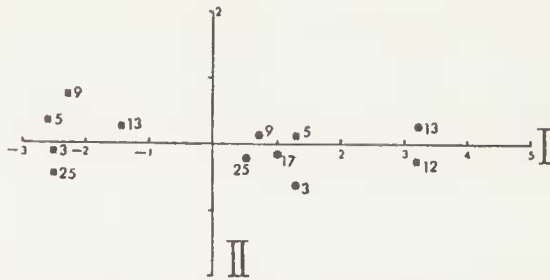


Fig. 14—Canonical analysis of variation in males of *Anthochaera chrysoptera* ■ and *A. carunculata* superspecies ●.

difference was found between the New South Wales, Nowra, Victorian, Tasmanian and Fleurieu Peninsula populations (5, 7, 9, 13, 17), although with the females (Fig. 13) these last two populations show slightly greater divergence from the Victorian (9) populations.

The Flinders Is., King Is. and SW. Australia populations (11, 12, 25) diverge from the geographically nearest populations (Vict., Tasm. and Fleurieu Peninsula 9, 13, 17).

P. novaehollandiae and *P. nigra* are sympatric in New South Wales and SW. Australia, but in Queensland *P. nigra* occurs alone. Surprisingly, it is the SW. Australian population of *P. nigra* that differs far more markedly from the Queensland population and not the New South Wales population.

Salomonsen (1967) recognized four subspecies of *P. novaehollandiae*: from Queensland-New South Wales-Victoria-S. Australia; Bass Strait islands; Tasmanian mainland and SW. Australia. This study supports his scheme, except that the King and Flinders Islands populations may be subspecifically distinct. With *P. nigra*, Salomonsen (1967) recognized one subspecies in Queensland-New South Wales, and another in SW. Australia. My analysis supports this.

Anthochaera chrysoptera and *A. carunculata* superspecies

The Tasmanian (13) population of *A. chrysoptera* clearly diverges from the geographically closest population (Victoria 9) for males (Fig. 14), although this is not as pronounced with females (Fig. 15). Generally, the mainland populations show little divergence from one another, with geographically close

populations being most alike. However, with males, the Queensland and SW. Australian populations (3, 25) converge in morphological variation (Fig. 14). With females, the SW. Australia (25) population diverges markedly from the nearest available population (SE. South Australia).

The populations of *A. carunculata* (from mainland Australia) all fall near one another, whereas those of *A. paradoxa* (12, 13) show marked divergence from the nearest mainland population (Victoria 9). Only Tasmania and King Is. share *A. paradoxa*.

Salomonsen (1967) accepted four sub-

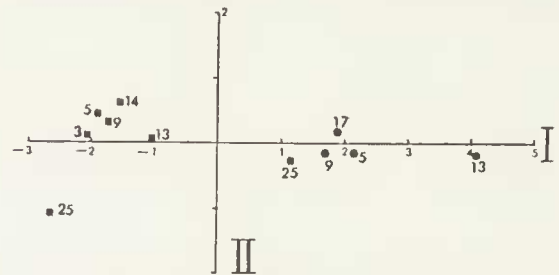


Fig. 15—Canonical analysis of variation in females of *Anthochaera chrysoptera* ■ and *A. carunculata* superspecies ●.

species of *A. chrysoptera* (SW. Australia, Kangaroo Is., Tasmania, and rest of range), two of *A. carunculata* (SW. Australia, and elsewhere), and none of *A. paradoxa*. Possibly only the Tasmanian and SW. Australian ones for *A. chrysoptera* are worth recognizing. It is also possible that *A. paradoxa* is a well-marked subspecies of *A. carunculata* (see Discussion).

Petroica cucullata superspecies

The Tasmanian mainland (13), King Is. (12) and Flinders Is. (11) populations (*P.*

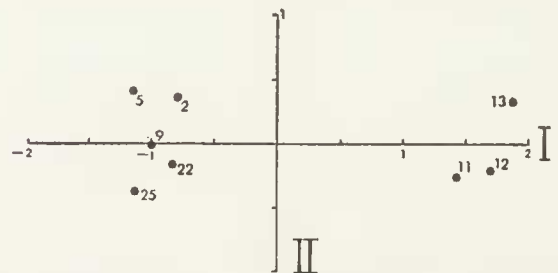


Fig. 16—Canonical analysis of variation in males of *Petroica cucullata* superspecies.

vittata) greatly diverge from the mainland populations (*P. cucullata*) (Figs. 16-17). The mainland points fall close to one another, with geographically close populations showing similar variation. Populations at the extremes of range (e.g. SW. Australia 25, and New South Wales 5) show greater dissimilarity. The Bass Strait islands and Tasmanian mainland (11, 12, 13) populations show about as much variation among themselves as do the mainland populations. The Tasmanian (13) population falls closest to the King Is. (12) population (Figs. 16-17).



Fig. 17—Canonical analysis of variation in females of *Petroica cucullata* superspecies.

With females (Fig. 17), the same trends apply except that the difference between the New South Wales (5) and SW. Australia (25), and the Tasmania (13) and Flinders Is. (11), populations are more pronounced. Presumably such changes reflect sexual dimorphism.

Eopsaltria georgiana and *E. australis*

E. georgiana (■ 25) is endemic to SW. Australia and is regarded as the senior member of a double invasion with *E. australis* (Keast 1961). It shows marked divergence from all other populations (Figs. 18-19). *E. australis* was formerly regarded as consisting of two species (Mathews 1930). These were *E. australis* sens. str. from E. Australia, W. to SE. Australia, and *E. griseogularis* from SW. Australia and Eyre Peninsula.



Fig. 18—Canonical analysis of variation in males of *Eopsaltria georgiana* ■ and *E. australis* ●.



Fig. 19—Canonical analysis of variation in females of *Eopsaltria georgiana* ■ and *E. australis* ●.

The *E.* coast forms fall close together, with geographically close populations falling very near to one another (Fig. 18). The SW. Australia (25) and Eyre Peninsula (19) populations do show divergence from *E.* coast populations (1, 2, 5, 9), but it is uncertain whether they are specifically or subspecifically distinct. With females (Fig. 19), the SW. Australia (25) and Eyre Peninsula (19) populations show a much more pronounced dissimilarity from the *E.* coast ones. Also, the Queensland populations are more different from the New South Wales and Victorian populations.

Gymnorhina tibicen

The genus *Gymnorhina* was formerly separated into two or more species (Mathews 1930), a black-backed form from the N. parts of Australia (*G. tibicen*) and a white-backed form from southern Australia, including Tasmania (*G. hypoleuca*). Condon (1969) recognizes only one species because extensive hybrid

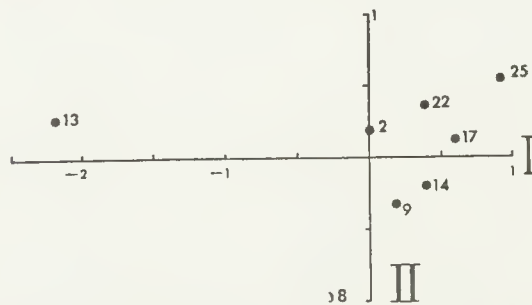


Fig. 20—Canonical analysis of variation in males of *Gymnorhina tibicen*. Point 22 refers to black-backed individuals (see map of distribution in Condon (1969)).

zones occur in S. Australia and Victoria. *Gymnorhina* is not native to the Bass Strait islands.

I found it necessary to lump sexes of the Tasmanian population because too few specimens were sexed and I could find no consistent

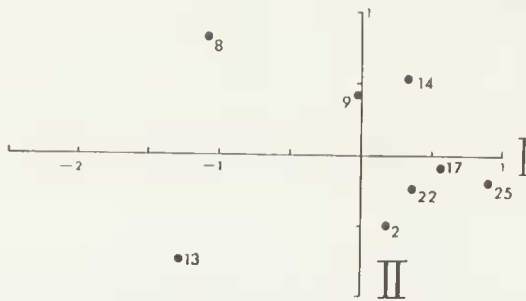


Fig. 21—Canonical analysis of variation in females of *Gymnorhina tibicen*. Point 22 refers to black-backed individuals.

differences between those specimens that were accurately sexed. The Tasmanian (13) population is clearly distinct from all others, even when compared with all male populations and all female populations (Figs. 20-21). That is, the lumping of the sexes has not obscured the distinctiveness. The Tasmanian population consists of smaller individuals.

Geographically near populations exhibit similar morphological variation (Figs. 20-21). Because appropriate comparisons should always be with the nearest population, much variation is not worth naming on the basis of morphological differences. Thus, the SW. Australia (25) point falls closest to the black-backed (22) and white-backed (17) populations in S. Australia, and so on. However, the S. Queensland (2) population falls nearer to the S. Australian (22) population than to the geographically nearer Canberra (8) population. The Canberra population shows a marked divergence from the Victorian (9) population. The Victorian population is almost exclusively made up of white-backed birds whereas the Canberra population consists of about equal numbers of white- and black-backed birds. Possibly character displacement between white- and black-backed birds accounts for the unexpected position of the Canberra point.

Amadon (1962) recognized nine subspecies of *Gymnorhina*. Those in S. and E. parts of Australia were *G. t. dorsalis* (SW. Australia), *G. t. hypoleuca* (Tasmania), *G. t. leuconota* (South Australia and S. Victoria), and *G. t. tibicen* (S. Queensland, New South Wales including Canberra district, N. Victoria and N.

parts of S. Australia). My study suggests that the morphological variation among populations is too complex to explain with these names.

Strepera graculina superspecies and
S. versicolor superspecies

S. graculina and *S. fuliginosa* form a superspecies, the former being found in E. Australia and Lord Howe Is., and the latter being found only on King Is., Flinders Is. and Tasmania. *S. versicolor* and *S. arguta* form another superspecies, with the former being found in SE. and southern Australia and the latter only on Tasmania.

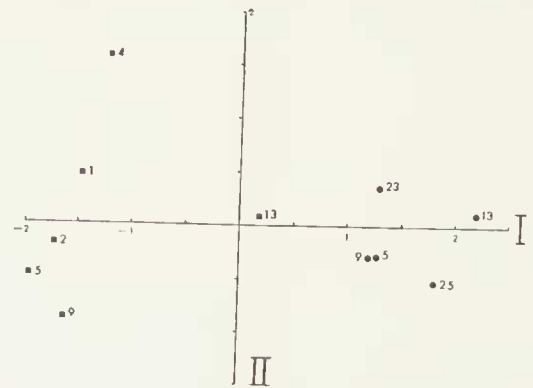


Fig. 22—Canonical analysis of variation in males of *Strepera graculina* superspecies ■ and *S. versicolor* superspecies ●.

S. fuliginosa from Tasmania (13) is clearly intermediate in morphology between *S. graculina* (1, 2, 4, 5 and 9) and *S. versicolor* (5, 9,

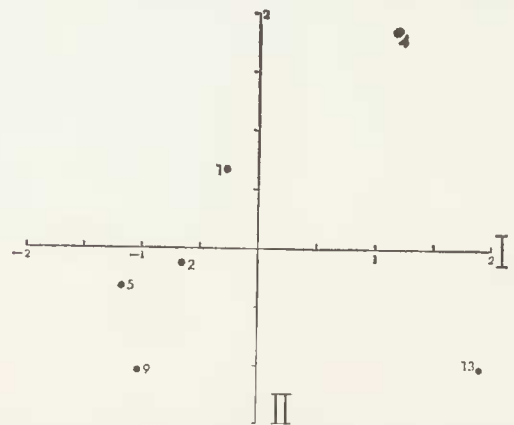


Fig. 23—Canonical analysis of variation in males of *Strepera graculina* superspecies.

13, 23, 25) (Fig. 22). Considering the *S. graculina* superspecies alone (Fig. 23), it is clear that three of the mainland points (Victoria, New South Wales and SE. Queensland 9, 5 and 2) fall near one another. The three isolated populations diverge in different degrees from these. The N. Queensland (1) population is least divergent, and is probably only recently isolated from that of SE. Queensland. The Lord Howe (4) point is as far from the SE. Queensland (2) point as is the Tasmania (13) point from the Victoria point (9), indicating that the distance per se of these islands from the adjacent mainlands is unimportant. These trends hold also for the female populations (Fig. 24). The King Is. (12) point falls near the Tasmanian (13) point.

Clearly, the Tasmanian, King Is., Lord Howe Is. and N. Queensland populations do show a degree of difference in variation that is worthwhile recognizing and naming. This contrasts with Amadon (1962), who recognized four superspecies of *S. graculina*, from Queensland, New South Wales, Victoria and Lord Howe Is. He recognized no subspecies of *S. fuliginosa*, and suggested that *S. fuliginosa* may only be a race of *S. graculina* (see Discussion).

Because of many unsexed specimens and a lack of clearcut differences between those that were sexed, I had to lump sexes for the Victorian and New South Wales populations of *S. versicolor*. The points (9, 5) or these populations fall very close (Figs. 22-25). The



Fig. 24—Canonical analysis of variation in females of *Strepera graculina* superspecies.

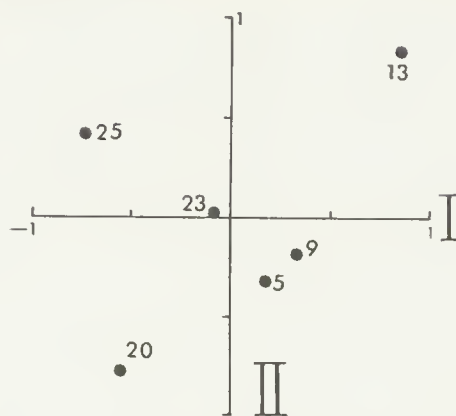


Fig. 25—Canonical analysis of variation in females of *Strepera versicolor* superspecies.

points for the race *S. v. melanoptera* (23) (found in S. Aust. E. of Gulf St Vincent and in W. Vict.), *S. v. intermedia* (20) (found on Eyre and Yorke Peninsulas) and *S. v. plumbea* (25) (of SW. Australia) all diverge from the E. coast points. The Tasmanian (13) population also diverges from the Victorian (9) population (Figs. 22-25).

Amadon (1962) treated *S. arguta* as a subspecies of *S. versicolor*, and recognized six other subspecies. These are from New South Wales-E. Victoria, SW. Australia, NW. Victoria, Kangaroo Is. and S. Australia E. of Gulf St Vincent, S. Australia W. of Gulf St Vincent, and Central Australia. The results for the populations studied here support such divisions.

Conclusions and Discussion

The general aim of any taxonomic study is to discover the relationships that exist among populations, and in particular whether patterns of variation are best described on a subspecific or specific level. An accurate knowledge of which populations are species or subspecies is obviously basic to any subsequent study using lists of species, such as biogeography.

This study indicates clearly how slight transcontinental variation within a species or subspecies compares with variation effected by isolation. All species with representatives on the Tasmanian mainland and/or the Bass Strait islands show differences in morphology from populations on nearby mainland Vic-

toria. The problem is whether such differences are worthy of specific recognition (see later).

In all but three cases (*Petroica vittata*, *Gymnorhina tibicen* and *Acanthorhynchus tenuirostris*) species on the Tasmanian mainland and/or Bass Strait islands show a nett increase in size of the six characters studied. The causes of such shifts are discussed elsewhere (Abbott 1972).

In many cases (e.g. *Gymnorhina tibicen*, *Eopsaltria australis*, *Phylidonyris nigra* and *P. novaehollandiae*, and *Melithreptus lunatus*) presently isolated populations in SW. Australia differ in various degrees from their conspecifics in E. Australia. The E. Australian populations are generally much alike in their variation.

It was found that out of the six cases for which I have samples from the Tasmanian mainland, King Is. and Flinders Is., the affinities of the Tasmanian population lie in four cases with the King Is. population, and in two with Flinders Is. This is very surprising, because geomorphological history of the Bass Strait area suggests that populations on Flinders Is. had about 4,000 years more than King Is. during which gene flow with the Tasmanian mainland could have occurred (Abbott 1973). The anomaly can perhaps be explained by assuming that the climate and ecology of King Is. more closely resemble that of the Tasmanian mainland than Flinders Is. This is true for rainfall (Hope 1969). Relevant to this point is that *Acanthiza pusilla*, *Acanthornis magnus* and *Anthochaera paradoxa* are on King Is. and the Tasmanian mainland but not on Flinders Is.

In general, the range of variation relative to the scale in Figs. 1-25 is much less than that found in other multivariate studies. Reeve's data (1941 and in Seal 1966) show a range of differences between means of each variate of 106-138, 110-140 and 37-51 mm respectively. Hope's data (1969) similarly show large ranges: e.g. her variate BAL ranges from 65 to 80 mm and LP4 from 5.6 to 7.8 mm. Most of the data used in this study show a much smaller range of variation, e.g. bill length for *Malurus cyanus* varied from 8.47 to 10.03 mm and wing length from 50.48 to 55.65 mm.

This being so, it is therefore all the more remarkable that any differences are evident.

There is a curious and largely untested apparent convention implicit in much Australian bird taxonomy. When an isolated population is made up of individuals of a different plumage from individuals in unisolated populations, that population has been deemed to be specifically distinct. As with most things in Australian ornithology, the convention seems to have been started by Gould. He wrote 'On comparing examples from Tasmania with others killed on the continent of Australia, a difference is found to exist in their relative admeasurements, the Tasmanian birds being more robust and larger in every respect; still as not the slightest difference is observable in the markings of their plumage, I consider them to be merely local varieties and not distinct species' (Gould 1865: 574-5).

Examples of such supposed species are *Acanthorhynchus superciliosus* (SW. Aust. representative of *A. tenuirostris*), *Strepera fuliginosa* (Tasm. mainland and Bass Strait islands representative of *S. graculina*), *S. arguta* (Tasm. mainland form of *S. versicolor*), *Malurus splendens* (SW. Aust. representative of *M. cyaneus*), *Sericornis humilis* (Tasm. mainland and Bass Strait islands representative of *S. frontalis*) and *Petroica vittata* (Tasm. mainland and Bass Strait islands form of *P. cucullata*).

However, whenever isolated populations do not differ strikingly in plumage (but usually in measurements of bill or wing), recent taxonomists have also preferred to give such populations mere subspecific status. Examples are *Phylidonyris novaehollandiae* and *P. nigra* in SW. Australia, *Anthochaera chrysoptera* in SW. Australia and Tasmania, *Melithreptus lunatus* in SW. Australia, *Acanthorhynchus tenuirostris* in Tasmania, and *Gymnorhina tibicen* in Tasmania (in Gould's time some of these were even ranked as species).

Taxonomists have not always been consistent, thus giving the impression their criteria for species and subspecies are arbitrary. Thus, *Strepera arguta* on Tasmania has normally been accepted as a full species. Yet the populations of *Strepera* in S. Australia and SW.

Australia have a similar degree of difference from *S. versicolor* of E. Australia, and now they are treated as being only subspecifically distinct by the latest revisor, Amadon (1962). Either *S. arguta* is a subspecies of *S. versicolor* (Amadon's conclusion) or the S. and SW. Australian forms are species (as partly treated by RAOU, 1926). A similar situation could be argued for many of the forms studied in this paper.

Plumage should be as good, or as bad, an indicator of subspecific status as other (e.g. morphometric) differences. Because the only unequivocal test of whether two allopatric populations are different species is whether significant interbreeding takes place after they meet in nature (Mayr 1963), it is not possible to properly evaluate the taxonomic status of some of the populations studied in this paper (e.g. *Malurus cyaneus* on the Tasmanian mainland and Bass Strait islands, *Acanthiza pusilla* on Tasmania, *Melithreptus lunatus* in SW. Australia). One celebrated example concerns *Acanthiza ewingi*. If *Acanthiza pusilla* were not present in Tasmania, then *Acanthiza ewingi* being so similar in plumage and morphology (Figs. 4-5) to *A. pusilla* in Victoria would be given subspecific status. The fact that *A. ewingi* and *A. pusilla* come into contact on the Tasmanian mainland and on King Is. without interbreeding surely indicates that they are specifically distinct (Mayr 1942). Similarly, if it were not that *Pardalotus punctatus* and *P. xanthopygus* are sympatric in the Mount Lofty Ranges, and that *Melithreptus lunatus* and *M. albogularis* are sympatric near Brisbane, these species would today be ranked as subspecies, as was done in both cases by Mathews (1930), and in the second case by Rand and Gilliard (1967). Also, White (1790) records, presumably from similarity in plumage and difference in size, that *Anthochaera carunculata* and *A. chrysoptera* are the male and female of one species, and also that *Phylidonyris novae-hollandiae* and *P. nigra* are the sexes of one species. It was not until the 'sexes' were found not to interbreed that it was realized that each 'sex' is a good species.

However, the immediate needs of the bio-

logist for the correct name for a population of birds means that the taxonomist has to resort to a less satisfactory criterion. This is best reached when as many characters as possible are considered when making taxonomic judgement.

As rightly pointed out by Oliver (1955), the phrase 'potentially interbreeding natural populations' in Mayr's definition of a species destroys the utility of that definition, because it puts the determination of a form as a species or subspecies back to opinion. This may mean that the modern trend to merge species, though convenient, may not be biologically correct. That is, many forms in SW. Australia and Tasmania, etc., which are at present treated as subspecies may really be species.

The excessive use of subspecific designations has been commented on by many workers (e.g. Serventy 1950, Wilson and Brown 1953). Although it has always been fashionable to deride the work of G. M. Mathews, it is scarcely appreciated that he used concepts that nearly all other workers of his day did (e.g. Ridgway, Bowler Sharp). I think that the enormous collection of skins from all over Australia built up by Mathews enabled him to describe so many new subspecies. Indeed, replying to criticism of his technique, Mathews noted that a large number of his subspecies would even be granted specific rating by some fellow-workers (Mathews 1912). Another reason is that very early workers, such as Latham and Shaw but chiefly Gould, had named many of the populations found at the extremes of species ranges. It remained for the workers in the first few decades of this century, such as Campbell and Mathews, to name the intermediate populations, before the concept of clinal variation had been articulated by Huxley (1942). My study suggests that even many of the trinomials in present use could be dispensed with, because patterns of variation are too complex to be worth naming.

A main aim of my research has been to examine how the results of an intuitive analysis of population variation compare with those from a more objective analysis (my analysis is subjective in the choice of the variables

measured, but more objective in the way that these measurements are analysed). The main objection to an intuitive analysis of taxonomic problems is that it is not consistent, as given a similar degree of variation between populations, they may either be ranked as different subspecies or different species.

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Appendix

Sample sizes. The first number of each pair is the locality, the second is the number of specimens measured.

Malurus cyaneus

♂: 3, 25; 5, 101; 9, 51; 11, 17; 12, 27; 13, 65; 14, 11; 16, 13; 17, 25; 18, 13; 19, 8. Total: 356 specimens.

Malurus splendens

♂: 25, 52. Total: 52 specimens.

Sericornis frontalis superspecies

♂: 3, 14; 5, 36; 9, 31; 11, 17; 12, 20; 13, 39; 17, 9; 18, 10; 25, 50; 26, 11. Total: 237 specimens.

♀: 3, 9; 5, 22; 9, 16; 11, 12; 12, 7; 13, 13; 17, 10; 25, 47; 26, 11. Total: 147 specimens.

♂ + ♀: 10, 10. Total: 10 specimens.

Acanthiornis magnus

♂ + ♀: 13, 17. Total: 17 specimens.

Acanthiza pusilla superspecies

♂: 3, 10; 5, 19; 6, 14; 9, 28; 13, 28; 14, 19; 17, 12; 18, 10; 19, 9; 25, 46. Total: 195 specimens.

♀: 3, 5; 5, 8; 6, 14; 9, 6; 13, 17; 17, 5; 18, 5; 25, 22. Total: 82 specimens.

♂ + ♀: 21, 10. Total: 10 specimens.

Acanthiza ewingi

♂: 11, 9; 12, 13; 13, 32. Total: 54 specimens.

♀: 11, 6; 12, 7; 13, 12. Total: 25 specimens.

Acauthorhynchus tenuirostris superspecies

♂: 3, 9; 5, 22; 7, 22; 9, 19; 13, 24; 17, 7; 25, 55. Total: 158 specimens.

♀: 5, 25; 7, 25; 9, 10; 13, 20; 17, 5; 25, 16. Total: 101 specimens.

Melithreptus lunatus superspecies

♂: 3, 21; 5, 21; 9, 24; 13, 41; 17, 9; 25, 52. Total: 168 specimens.

♀: 3, 15; 5, 15; 9, 7; 13, 23; 25, 33. Total: 93 specimens.

Melithreptus gularis superspecies

♂: 3, 5; 9, 6; 12, 7; 13, 21. Total: 39 specimens.

Meliphaga leucotis superspecies

♂: 3, 9; 5, 26; 6, 27; 9, 29; 11, 7; 12, 9; 13, 47; 15, 13; 18, 8; 19, 7; 25, 11. Total: 193 specimens.

♀: 3, 5; 5, 21; 6, 19; 9, 15; 12, 6; 13, 38; 15, 9; 19, 6; 25, 6. Total: 125 specimens.

Phylidonyris novaehollandiae

♂: 5, 31; 7, 25; 9, 23; 11, 6; 12, 18; 13, 43; 17, 14; 25, 41. Total: 201 specimens.

♀: 5, 19; 7, 25; 9, 20; 12, 7; 13, 21; 17, 8; 25, 27. Total: 127 specimens.

♂ + ♀: 3, 6. Total: 6 specimens.

Philidonyris nigra

♂: 3, 26; 5, 36; 25, 16. Total: 78 specimens.

♀: 3, 5; 5, 19; 25, 8. Total: 32 specimens.

Anthochaera carunculata superspecies

♂: 3, 11; 5, 19; 9, 24; 12, 5; 13, 39; 17, 8; 25, 24. Total: 130 specimens.

♀: 5, 20; 9, 13; 13, 23; 17, 11; 25, 18. Total: 85 specimens.

Anthochaera chrysoptera

♂: 3, 7; 5, 16; 9, 5; 13, 22; 25, 15. Total: 65 specimens.

♀: 3, 5; 5, 16; 9, 8; 13, 18; 14, 7; 25, 18. Total: 72 specimens.

Petroica cucullata superspecies

♂: 2, 14; 5, 36; 9, 15; 11, 7; 12, 16; 13, 28; 22, 21; 25, 15. Total: 152 specimens.

♀: 5, 21; 11, 7; 12, 13; 13, 16; 21, 5; 22, 11; 25, 11. Total: 84 specimens.

Eopsaltria australis

♂: 1, 13; 2, 41; 5, 49; 9, 38; 19, 10; 25, 57. Total: 208 specimens.

♀: 1, 13; 2, 14; 5, 29; 9, 8; 14, 7; 19, 5; 25, 31. Total: 107 specimens.

Eopsaltria georgiana

♂: 25, 23. Total: 23 specimens.

♀: 25, 15. Total: 15 specimens.

Gymnorhina tibicen

♂: 2, 16; 8, 22; 9, 22; 14, 9; 17, 16; 22, 12; 25, 22. Total: 119 specimens.

♀: 2, 16; 8, 22; 9, 15; 14, 6; 17, 20; 22, 7; 25, 29. Total: 115 specimens.

♂ + ♀: 13, 29. Total: 29 specimens.

Strepera graculina superspecies

♂: 1, 7; 2, 13; 4, 7; 5, 24; 9, 11; 13, 17. Total: 79 specimens.

♀: 1, 8; 2, 9; 4, 7; 5, 5; 12, 6; 13, 10. Total: 45 specimens.

Strepera versicolor superspecies

♂: 13, 11; 23, 16; 25, 27. Total: 54 specimens.

♀: 13, 11; 20, 7; 23, 15; 25, 27. Total: 60 specimens.

♂ + ♀: 5, 25; 9, 22. Total: 47 specimens.